TREE SELECTION THEORIES SUPPORTED BY 22 YEAR RECORD

C. R. Struble,
U. S. Department of Agriculture,
Bureau of Entomology and Plant Quarantine

19417

INTRODUCTION

Time is an important element in the completion of studies that concern the growth and life of a forest. This is equally true of entomological studies that stem out of the basic environmental conditions that render forest trees susceptible to bark beetle attack. Theories that explain the susceptibility of trees to bark beetle attack are easily conceived of, but their final proof must await the test of years.

One of the earliest theories developed in forest entomology was concerned with tree selection by bark beetles. The character of kill, particularly in ponderosa pine stands, indicated that perhaps the slower growing trees and those on the poorer sites were first selected for attack by the western pine beetle, Dendroctonus brevicomis Lec. In 1925 I. L. Person put this theory to an actual test, on what is known as the Cascadel Tree Selection Plot, located in the westside ponderosa pine type in the Sierra National Forest. The records upon which this study is based extend back to 1919 so that the entire plot data now covers a period of 22 years. The writer has recently completed an analysis of the accumulated data in order to bring this particular plot study to a close. From this material we are now able to judge how well the original theories have worked out over a fairly long period of time.

The ideas underlying the plot study by Person were first expressed in published literature by Craighead and Miller. In 1925 Craighead1/ stated: "General observations indicate that the western pine beetle normally attacks the more slowly growing trees, although measurements of a sufficient number of infested trees to verify this have not been compiled." Also, "Generally speaking, the western pine beetle appears to prefer overmature, slow-growing, decadent trees, particularly those on the poorer sites".

1/ Craighead, F. C. 1925. The Dendroctonus Problems. Journal of Forestry, Vol. XXII, No. 4: April, 1925; pp 340-354.

Again in 1926 Miller2/ stated: "Studies which have recently been carried on by H. L. Person indicate that under endemic conditions the western pine beetle shows a decided tendency to select and kill the more slowly growing trees of the stand. It is in trees of slow growth rate that it usually builds up in numbers and becomes aggressive. Once it has become abundant, it attacks with much less discrimination and kills vigorous as well as slow growing trees by sheer force of numbers. However, the mortality of the beetles when attacking fast-growing trees is high, so that as a rule epidemics are short-lived in stands where fast-growing trees predominate. These discoveries open up the possibility of reducing losses through logging practices and of taking out most of the susceptible trees in the marking practice on sale areas so as to leave only the more resistant trees for seeding purposes and future cuts".

2/ Miller, J. M. 1926. The Western Pine Beetle Control Problem. Jour. of Forestry, Vol. XXIV, No. 8; pp 897-910.

Later in 1928 Person3/ published an article in which he defines the theories that were considered in setting up the Cascadel tree selection plot and presents the results of his preliminary studies.

3/ Person, H. L. 1928. Tree Selection by the Western Pine Beetle. Journal of Forestry, Vol. XXVI, No. 5: pp 564-578.

DESCRIPTION AND HISTORY OF THE CASCADEL PLOT

This is the oldest plot in the ponderosa pine region on which studies of insect kill have been continued.. It is situated in the central Sierra subregion near North Forek, California at an elevation of 3,500 feet.. In area it is one mile long by 1/8 of a mile wide, containing 80 acres, and is part of the Cascadel basin of virgin ponderosa pine (Sites II, III, and IV).. The long axis runs north and south to traverse ridges and draws of a moderately steep west slope. A variety of slopes, exposures, and growing conditions are represented.. Growing conditions as a whole are typical of westside (Sierra) ponderosa pine lying between fringe and optimum type stands.

During the 22-year period from 1919 to 1941, western pine beetle infestations increased from low endemic conditions to high epidemic and then subsided again to low endemic conditions. The peak of the epidemic was reached in 1931, and the suddenness and intensity of this outbreak greatly surpassed any previous records of beetle activity in this region.

The original plot inventory, taken in 1926, included DBH measurements, crown condition, and descriptions by dominance for all trees over 12 inches DBH. Cores were taken from all recorded trees and measurements were made of annual rings dating from 1917 to 1926. Loss records were available from previous cruises of this plot area, running back to 1919. Continuous records were maintained throughout the period of the study. The final inventory was taken in 1941 when the increment was measured on trees of the original stand and in the poles which had come into merchantable size. From this available data we have been able to determine (1) the volume of beetle kill from 1919 to 1940 and net stand depletion since 1926, (2) the influence of diameter and growth rate on the selection of trees by the beetle, (3) the effect of epidemic and endemic conditions on the selection of trees by the beetle, (4) the relation of current growth rate to rise and fall of infestations, and (5) to a more limited extent, the significance of site selection.

EXTENT OF KILL 1919 TO 1940 AND STAND DEPLETION

Ponderosa pines killed by insects during this period amounted to 22 per cent of the total number and 28 per cent of the total volume[1] on the Cascadel plot. Over 50 per cent of this loss occurred during the years from 1929 to 1934. Approximately 82 per cent of the total volume was killed directly by the western pine beetle and 15 per cent by a combination of Ips confusus Lec. and the western pine beetle. The remaining 3 per cent was made up of falthead (Melanophila sp.) kills and unknown causes. Figures are presented in Table 1.

1/ The total stand, including living and insect killed trees, at the time the Cascadel plot was established in 1926 amounted to 1,470 trees having a volume of 1,169,410 board feet. These basic stand figures included all kill dating back to 1919.

Table 1. Distribution of Kill by Years

Year	Volume (Board Feet)	Number of Trees
1919	14,970	9
1920	1,180	2
1921	1,690	3
1922	5,540	6
1923	8,940	15
1924	1,460	3
1925	30,420	27
1926	4,800	9
1927	20,630	26
1928	3,820	3
1929	10,840	10
1930	21,030	21
1931	80,690	65
1932	42,060	42
1933	25,250	23
1934	10,720	17
1935	7,300	8
1936	13,390	10
1937	14,090	8
1938	7,400	2
1939	710	3
1940	3,530	2
Total	329,460	322

Part of this loss was offset by the increment of the original stand still living in 1940. An estimate of the amount in terms of board feet, determined from a 10 per cent sample and applied to the entire living original stand, amounted to 110,328 board feet. The volume killed during the same period amounted to 269,460 board feet. The net loss was, therefore, 150132 board feet, representing a net reduction of 13 per cent of the original volume living in 1926.

The effect of insects during this period has been to deplete the stand. This was partially compensated for by the growth of poles into merchantable sized trees during the period since the plot was established. In 1940, 403 new merchantable sized trees, having a volume of 58,670 board feet were recorded. As a result there are now 1,566 living merchantable sized trees, or 177 more than were present in 1926. The volume lost during the past decade may be largely compensated for by growth if the insect kill remains at its present low annual rate for the next 10 years. On the other hand, another severe epidemic would result in still further depletion.

RELATION OF DIAMETER AND GROWTH RATE TO TREE SELECTION

The preference for trees of intermediate diameters, from 20 to 30 inches DBH, was indicated by Person[3] on the basis of measurements of 5,000 trees killed by the western pine beetle. His data indicated that the number of killed trees within those diameters was much greater in proportion to the number of these diameters occurring in the total stand than for other diameter groups.

The selection of trees within intermediate diameter groups was again shown by the Cascadel plot data from 1926 to 1940, in which over 50 per cent of the trees killed ranged between 24 and 34 inches in diameter. Since the number of trees in this diameter range constitute approximately 1/3 of the total stand, it appears that there is a distinct preference for trees of intermediate diameter. This is apparently independent of any other factor.

Tree selection and kill by the beetle was found to correlate directly with growth rate as indicated by the width of annual rings.1/ The plot record, dating from 1927 to 1940, showed that 51 per cent of the slowest growing trees were killed (Table 2). This mortality per cent decreased rapidly with an increase in rate of growth.

1/ The average annual growth rate of trees during the period from 1917 to 1926 was used as a basis for determining the relation between growth rate and tree selection by insects in subsequent years.

Table 2. Distribution of Living and Insect Killed Trees by Growth Rate

Average Annual ring width (millimeters) 1917-1926	Living 1926	Died 1927-1940 No.	Died 1927-1940 %*	Living 1940
0.00-0.50	169	86	51	83
0.51-1.00	257	55	21	202
1.01-1.50	259	53	20	206
1.51-2.00	231	25	11	206
2.01-3.00	269	19	7	250
3.01-4.00	127	8	6	119
4.01-5.00	45	4	9	41
5.01-7.00	19	0	0	19
7.01-10.00	6	0	0	6

*Per cent of total trees in each growth rate group.

Among the trees selected, those with a radial increment of .50 millimeter or less per year amounted to 37 per cent of the total number killed and 6 per cent of the total trees in the stand. Thirty-three per cent of the trees with an annual ring width of 1.00 millimeter or less per year and comprising 10 per cent of the stand were killed. Moderate growing trees with annual rings from 1.00 to 2.00 millimeters wide comprised 31 per cent of the total number killed and 5 per cent of the total trees in the stand. Fast growing trees with rings wider than 2.00 millimeters per year comprised 12 per cent of the total number killed and 2 per cent of the total trees in the stand. Trees with annual rings wider than 5 millimeters per year were unattacked.

EFFECT OF EPIDEMIC ON GROWTH RATE SELECTION

The degree of tree selection was affected measurably by differences in beetle activity during endemic and epidemic conditions. Both conditions prevailed during the period of study on the plot and the number of trees killed was sufficient to provide an interesting and significant comparsion as shown by Table 3.

Table 3. Comparative Selection by Growth Rate Before, During, and After Epidemic

Average Annual ring width (millimeters) 1917-1926	Before Epidemic 1927-1929			During Epidemic 1930-1934			After Epidemic 1935-1940		
	Total trees	Died trees	Mortality Per cent*	Total trees	Died trees	Mortality Per cent*	Total trees	Died trees	Mortality Per cent*
0.00-0.50	169	10	5.9	159	58	36.4	101	18	14.9
0.51-1.00	257	6	2.3	251	42	16.7	209	7	3.2
1.01-1.50	259	3	1.1	256	45	17.6	217	5	2.1
1.51-2.00	231	1	0.4	230	21	9.0	209	3	1.6
2.01-3.00	269	1	0.3	268	14	5.2	254	4	1.7
3.01-4.00	127	1	0.8	126	7	5.5	119	0	0.0
4.01-5.00	45	0	0.0	45	4	8.9	41	0	0.0
Over 5.00	25	0	0.0	25	0	0.0	25	0	0.0

*Per cent of total number of trees in each growth rate group.

The most significant points revealed by this comparison are:

(1) The trees selected before the epidemic were predominantly of slow growth. Only an occasional tree growing faster than 1.00 millimeter per year was killed. The average growth rate of trees in this group was .80 millimeter.

(2) During the epidemic period from 1930 to 1934 there was still a strong preference for slower growing trees, but also a distinct tendency was evident for the beetles to spread their attacks among trees of more rapid growth. The average growth rate of all trees in this group was 1.19 millimeters.

(3) During the post epidemic period the preference for slow growing trees was well marked, but there was still considerable activity among trees growing as fast as 3 millimeters per year. This is probably due to increased populations of beetles following immediately after the epidemic and to the lessened numbers of slow growing trees left to attack.. The average growth rate of trees in this group was .84 millimeter.

RELATION OF CURRENT GROWTH RATE ON FLUCTUATING INFESTATIONS

Insect losses on the Cascadel plot were in some measure affected by the current growth rate of trees in the stand.. Data taken in 1941 from a 10 per cent sample of living trees in the original stand, strongly indicated that previous endemic and epidemic conditions were related to the growth pattern covering the years when these conditions prevailed. These data as illustrated by Figure 1, show that during the years immediately preceding the 1931 epidemic there was a sudden and rapid decline in growth rate. The same trend, to a lesser degree, was indicated in 1925, following the sudden decline in growth rate in 1924.. Conversely, when there was a rapid and sustained rise in growth rate, as occurred from 1935 to 1939, insect losses remained at a low level.

While a relationship between growth rate and the rise and fall of insect activity is indicated by these data, there are also certain inconsistencies. For example, the sudden decline in beetle losses following the 1931 epidemic occurred while the growth rate of the stand was still falling off. This indicates that some other factor may have been responsible, such as over-crowding of insect populations or a decrease in the number of susceptible trees.

THE SIGNIFICANCE OF SITE

Studies on the influence of site in the selection of ponderosa pines by the western pine beetle have given conclusive evidence that this factor is highly important. Person's evidence from 1,800 acres of the Cascadel unit revealed that heaviest losses were sustained on site IV and lightest on site II. Further confirmation of Person's evidence resulted from studies by the writer of 3 10-acre sub-plots, representing sites II, III, and IV respectively of the Cascadel tree selection plot at the peak of the epidemic in 1932.. It was found that the losses on the site IV plot amounted to 80 per cent of the total number of trees in the stand; on site III it was 14 per cent, and on site II the loss was 6 per cent.. From this evidence it is probably safe to conclude that the greatest insect hazard is found on the poorer sites.

DISCUSSION AND CONCLUSIONS

The conclusions that appear to be warranted as a result of this 22-year record are applicable primarily to the westside type ponderosa pine stands occurring mainly at elevations ranging between 2,500 and 4,500 feet, where there are many differences in site quality owing to ridges, draws and varying slopes and exposures which characterize this type. The behavior of western pine beetle infestations under these conditions tends to develop severe epidemics of short duration, with long intervals of relatively light losses between these sporadic outbreaks..

The Cascadel plot data have shown that: (1) sustained high losses over a period covering 2 decades have depleted the original stand volume by approximately 13 per cent; (2) that the greatest proportion of these losses occurred among trees having intermediate diameters (20-34 inches DBH); (3) that the majority of trees selected by the beetle were one millimeter or less in average radial increment for a 10-year period preceding death; (4) that during epidemic conditions there was a tendency to select faster growing trees on a diminishing scale from slow toward fast growth; (5) that the intensity of kill locally was correlated with site; (on site IV there were large groups, on site III small groups or scattered trees, and on site II an occasional killing).

From these supporting data we may therefore conclude:

1. That the western pine beetle selects and kills slow growing trees in preference to those of fast growth, but may spread its attacks among faster growing trees during epidemics when the supply of slow growing trees is reduced and the population of beetles is increased..

2.. That the poorer sites which occur locally on ridge tops, on dry south and west exposures, or on steep slopes, contain the great majority of susceptible trees and it is here that the western pine beetle concentrates activity, particularly during epidemics, when large groups of trees are killed..

While little has been added to the early theories that were advanced prior to this study, these conclusions do constitute a proof based upon 2 decades of study and records. The results of the Cascadel plot study are of further value in that they should serve as a basis for further efforts to distinguish susceptible trees in ponderosa pine stands of the westside (Sierra) type.. From a practical standpoint this may lead to a method of indirect control through the logging of susceptible trees, similar in its purpose to the "sanitation salvage" control that has been successfully developed for somewhat different site and growth conditions in the eastside pondersoa pine stands of northeastern California and Oregon..

FIGURE 1

AVERAGE GROWTH RATE OF 10 PER CENT SAMPLE OF ORIGINAL GREEN STAND FROM 1923 TO 1940 COMPARED WITH VOLUME OF TREES KILLED BY INSECTS DURING THIS PERIOD